
STUDIES IN NEOTROPICAL PALEOBOTANY. VIII. THE PLIOCENE COMMUNITIES OF PANAMA—INTRODUCTION AND FERNS, GYMNOSPERMS, ANGIOSPERMS (MONOCOTS)¹

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ABSTRACT

Thirty-one fossil spores and pollen of ferns, gymnosperms, and monocotyledonous angiosperms have been identified from the Pliocene Gatun Formation of Panama together with one unidentified Pyrrophyta. These are *Lycopodium* (types 1–4), *Selaginella*, *Alsophila*, *Cnemidaria*, *Cyathea* (types 1, 2), *Ophioglossum*, *Grammitis*, *Ceratopteris*, *Pteris* (types 1–5), other trilete fern spores (types 1, 2), *Ctenitis* (types 1–3), other monolete fern spores (types 1–5), *Podocarpus*, Gramineae, and Palmae (types 1, 2). Pollen of dicotyledonous angiosperms (51 types, including 13 with no previously known fossil records) and 27 unknowns presently under study make the Gatun assemblage one of the largest Tertiary floras in northern Latin America. The remaining descriptions and interpretation of the flora will be presented in concluding papers.

In 1962 the Panama Canal Commission drilled a series of wells in Gatun Lake as part of the Trinidad Dam Project to test the foundation for increasing the water storage capacity of the lake. Samples from along these cores were obtained by Elso Barghoorn in 1962 and by the author in 1963. The upper portions of the cores were used by Bartlett & Barghoorn (1973) for study of Quaternary sea level and climatic changes in central Panama during the past 12,000 years. The lower portions penetrated subsurface Gatun Formation sediments, and these samples serve as the basis for the present study. It is fortunate that samples were preserved because subsequently all cores drilled by the Commission, representing millions of years of vegetational and paleoenvironmental history, were discarded because of storage limitations. All known surface exposures of the Gatun Formation are marine sediments (Fig. 1), and the core material is presently the only source of data on the vegetation of Panama during Gatun time. Core SL-49 was drilled at latitude 9°80'N + 4,113, longitude 79°57'W + 1,987, and levels 222.5, 223, and 233.5 (in feet, following original log data) yielded plant microfossils. Core SL-103 was drilled at latitude 9°16'N + 5,945, longitude 79°52'W +

2,963, and levels 250, 253, 255.5, and 257 yielded plant microfossils. Numbers following latitude and longitude (e.g., + 4,113) are the number of feet between the minute cited (e.g., 80') and the next minute. They are used to locate precisely a site within a small or restricted locale.

The Gatun Formation was earlier assigned to the middle Miocene (Cooke et al., 1943; Stewart & Stewart, 1980; Woodring, 1957–1982), but marine invertebrate faunas now indicate a Pliocene age (Vokes, 1983; van den Bold, Stewart, pers. comm.). Other details on the location and geology of the Gatun and other Tertiary formations in Panama are summarized in Graham et al. (1985).

The Gatun Formation is the last and youngest in a series of five Tertiary pollen- and spore-bearing strata being studied from the Canal region of Panama. The others are the middle(?) to upper Eocene Gatuncillo Formation (Graham, 1985), and the lower Miocene Culebra, Cucaracha, and La Boca formations (Graham, 1988a, b, 1989). In addition, lower Miocene palynomorphs are known from the Uscari sequence of Costa Rica (Graham, 1987). Quaternary studies include those of Bartlett & Barghoorn (1973) on sediments from Gatun Lake, and Horn (1985) on sediments from DSDP site

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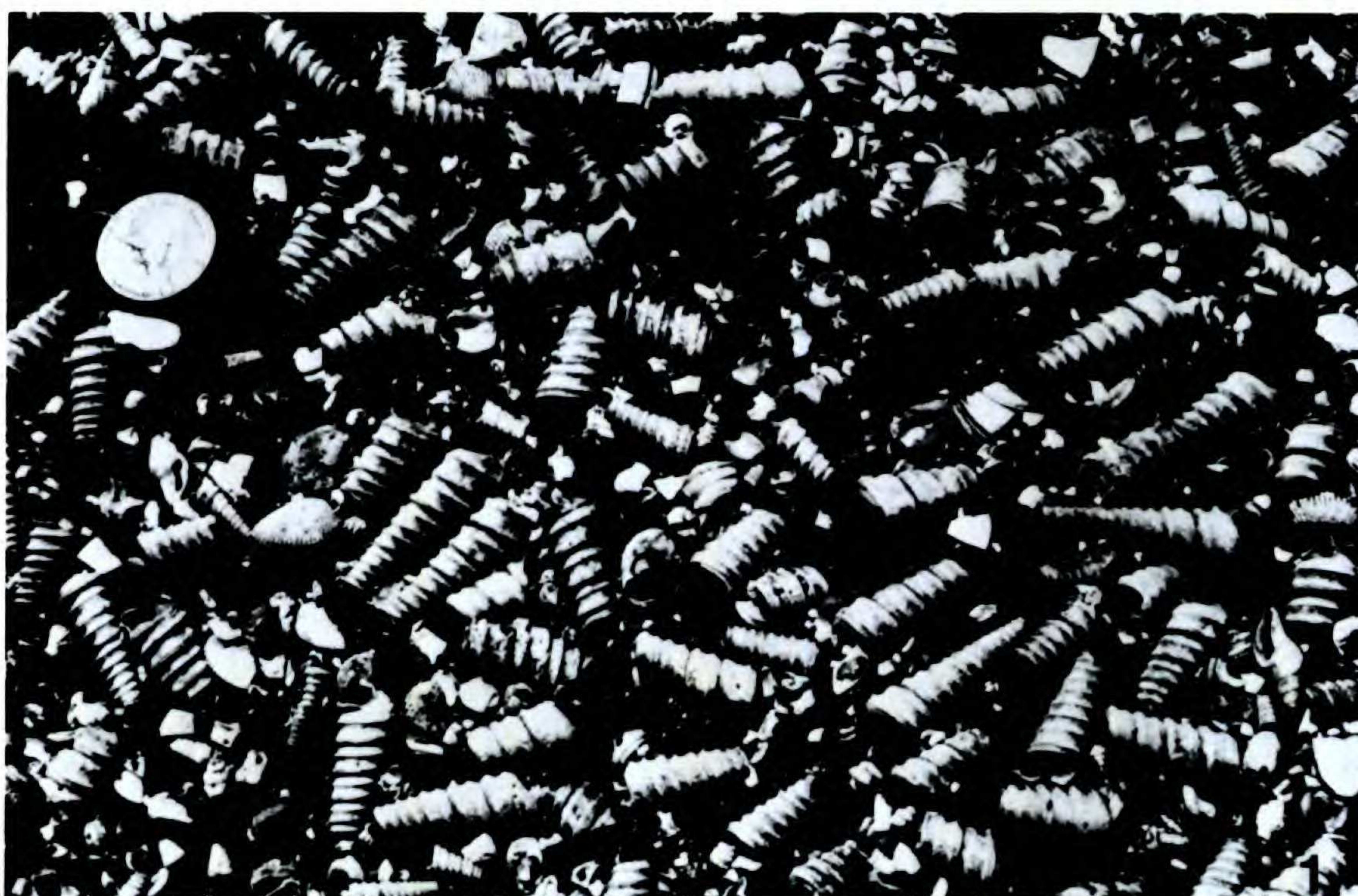


FIGURE 1. Surface outcrop of the Gatun Formation at Refinería Panama, near Colón, Panama. The dominant fossil is the marine gastropod *Turritella*. Several outcrops occur in the area, and all are marine sediments, lacking terrestrial plant microfossils. Terrestrial Gatun deposits are subsurface, and cores drilled by the Panama Canal Commission between 1950 and the 1960s have been discarded. Diameter of coin, 30 mm.

565 off western Costa Rica. In 1989, members of van der Hammen's group (pers. comm.) completed transects through the modern vegetation of Costa Rica preliminary to pollen and spore analysis of high-altitude peat deposits. Collectively, these studies will provide a more complete data base on Cenozoic vegetation and paleoenvironments for Panama and adjacent Costa Rica than for any other region of northern Latin America.

MATERIALS AND METHODS

Extraction and processing techniques are described in Graham (1985). Slides are labeled according to core number, depth, and slide number (e.g., SL-103, 253', 1). Location of the specimens on the slides is by England Slide Finder coordinates (e.g., ESF G-40). All materials are deposited in the palynology collections at Kent State University.

SYSTEMATICS

Thirty-one palynomorphs are described from the Gatun Formation. One unidentified Pyrrophyta (dinoflagellate) was also recovered. Several are common in other fossil floras, and for these the information is synoptic. Present ranges and ecological data are based primarily on Tryon & Tryon (1982) for ferns, and on Croat (1978) and D'Arcy (1987) for gymnosperms and monocots. General stratigraphic ranges for the Caribbean region follow Ger-

meraad et al. (1968) and Lorente (1986), with records from our previous studies listed separately. Other details on the systematics of the microfossils are discussed in Graham (1989: 51).

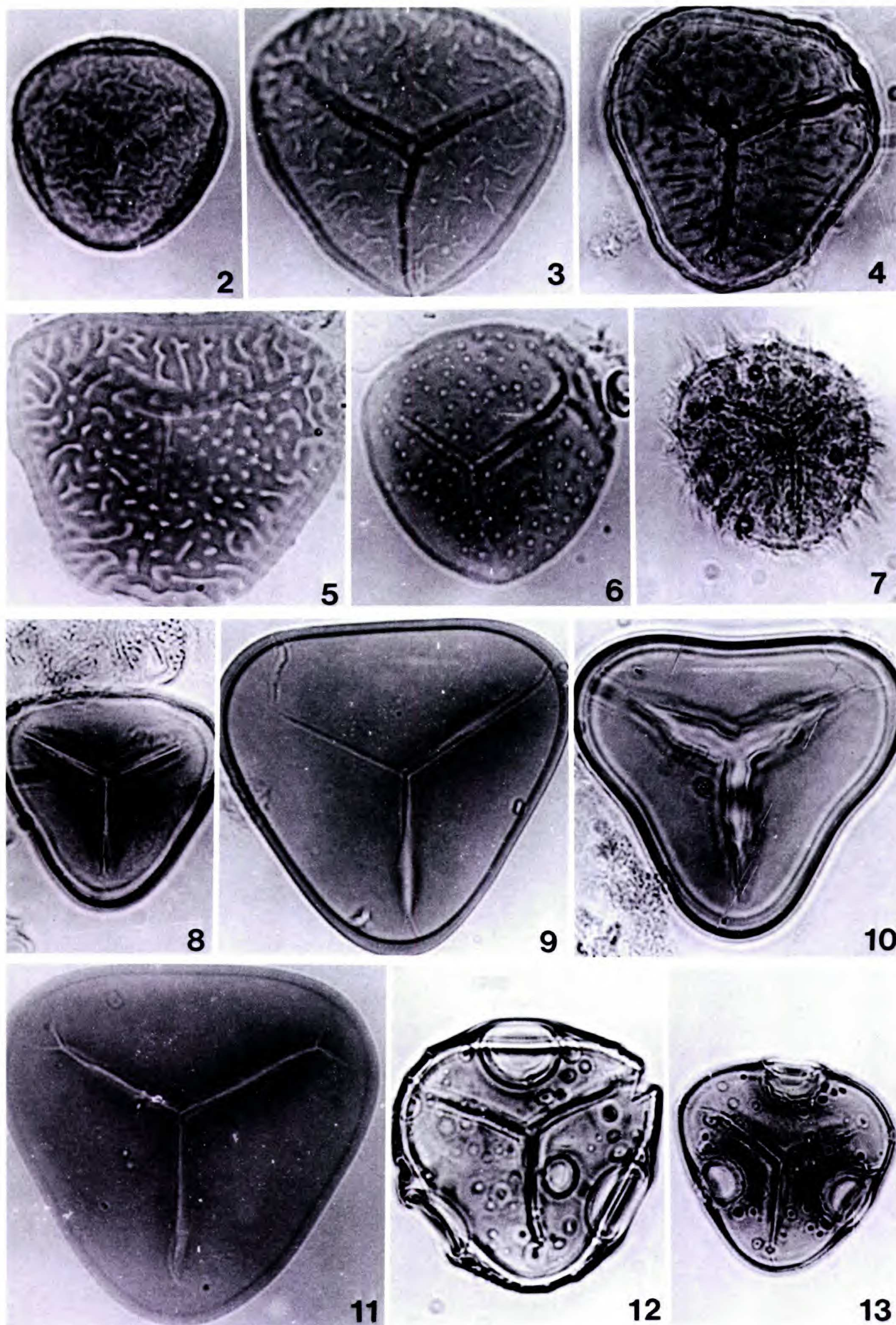
LYCOPODIACEAE

Lycopodium (type 1, Fig. 2). Amb oval-triangular to nearly circular, apices rounded; trilete, laesurae straight, narrow, ca. $12\ \mu\text{m}$ long, extending $\frac{2}{3}$ distance to spore margin, inner margin entire; distal surface reticulate, muri low, narrow (ca. $0.5\ \mu\text{m}$ wide), smooth, sinuous, lumina irregular, occasionally appearing as narrow, sinuous, slitlike openings as viewed through the spore from the proximal surface, proximal surface laevigate; wall $2\ \mu\text{m}$ thick, slightly thinner at apices; $36\text{--}39\ \mu\text{m}$.

The reticulate spores of *Lycopodium* are characteristic of subg. *Lycopodium* (Wilce, 1972; Tryon & Tryon, 1982: 807), but the Gatun specimens cannot be referred to any individual species.

Lycopodium (type 2, Fig. 3). Amb oval-triangular, apices rounded; trilete, laesurae straight, narrow, ca. $33\ \mu\text{m}$ long, extending to spore margin, inner margin entire; distal surface with narrow, sinuous slitlike openings, proximal surface laevigate; wall $3\ \mu\text{m}$ thick; $54\text{--}58\ \mu\text{m}$.

Lycopodium (type 3, Figs. 4, 5). Amb triangular to slightly concavo-triangular, apices rounded; laesurae straight, narrow, $22\text{--}24\ \mu\text{m}$ long,



FIGURES 2-13. Fossil spores from the Gatun Formation.—2. *Lycopodium* type 1, SL-103, 253' 4, ESF G-40.—3. *Lycopodium* type 2, SL-103, 253', 5, ESF L-22.—4, 5. *Lycopodium* type 3, SL-103, 253', 7, ESF K-21; SL-103, 253', 10, ESF P-26.—6. *Lycopodium* type 4, SL-103, 253', 4, ESF R-26.—7. *Selaginella*, SL-103, 253',

extending $\frac{3}{4}$ to nearly to spore margin; distal surface with low verrucae/rugulae to nearly flat surface with spaces in between appearing as circular to narrow, elongated, slitlike openings, proximal surface laevigate; wall 2–3 μm thick; 50–60 μm .

These spores are similar to those of subg. *Cer-nuistachys* (Wilce, 1972; Tryon & Tryon, 1982: 807), including such species as *L. (Huperzia fide Ollgaard, 1987) hippuredeum* Christ.

Lycopodium (type 4, Fig. 6). Amb oval-triangular to nearly circular, apices rounded; trilete, laesurae straight, narrow, ca. 18 μm long, extending $\frac{3}{4}$ to nearly to spore margin, inner margin entire; distal surface foveolate, pits circular, 0.5 μm to slightly less in diameter, moderately dense, evenly spaced, proximal surface laevigate; wall 2 μm thick; 45–50 μm .

These spores are similar to those of subg. *Selago* (Wilce, 1972; Tryon & Tryon, 1982: 807), including *L. linifolium* L.

There are about 125 species of *Lycopodium* in the Neotropics growing as terrestrial or pendant epiphytes in a variety of habitats, including wet to damp sites in savannas, rainforests, cloud forests, and paramo.

The stratigraphic range for the various types of *Lycopodium* spores has not been summarized. Spores of *Lycopodium* have been reported previously in our studies from the San Sebastian, Us-cari, Culebra, La Boca, and Paraje Solo formations.

SELAGINELLACEAE

Selaginella (Fig. 7). Amb oval-triangular to nearly circular, apices rounded; trilete, laesurae straight, narrow, ca. 12–15 μm long, extending $\frac{3}{4}$ to completely to spore margin, inner margin entire; distal surface echinate, spines ca. 3–6 μm long, base broad, occasionally giving reticulate appearance to spore surface, proximal surface laevigate to sparsely and minutely echinate; wall 2 μm thick; 30–38 μm (excluding spines).

There are about 250 species of tropical American *Selaginella*, growing primarily in mesic, damp, shaded forests and oak–pine woods, usually at elevations between sea level and 1,500 m, but with some species extending to 4,000 m (Tryon & Tryon, 1982: 820).

Spores of the *Selaginella* type are known in the stratigraphic literature as *Echitriteles* and range from Paleozoic to Recent. They are present in low percentages in the Gatuncillo, San Sebastian, Us-cari, Culebra, Cucaracha, La Boca, and Paraje Solo formations.

CYATHEACEAE

Alsophila (Figs. 8–11). Amb triangular, apices rounded; laesurae straight, narrow, ca. 18 μm long (in smaller specimens, to ca. 28 μm in larger ones), inner margin entire, bordered by lip 4–6 μm wide, outer margin of lip frequently bordered by small (0.5 μm or less), circular pits; laevigate; wall 2 μm thick; 45–65 μm .

This description is based on the type illustrated in Figure 8, which is the most common one recovered from the Gatun sediments. Variations include larger size (Fig. 9), lip faint (Fig. 11) to nearly absent (Fig. 9), pits bordering laesurae faint to conspicuous, laesurae closed (Fig. 9) or open (Fig. 10), and occasional branching of the laesurae apices (Fig. 11).

The designation of fossil spores as *Alsophila* vs. *Cyathea* is almost arbitrary because of the differing classifications of tree ferns (e.g., Holttum 1964, 1965; Tryon, 1970; Tryon & Tryon, 1982: 182) and the consequent labeling of herbarium specimens from which spore reference material is obtained. Laevigate or nearly laevigate fossil spores are provisionally referred to *Alsophila*, while micropunctate ones (Fig. 14) are referred to *Cyathea* (Graham, 1989: 55).

Alsophila is a genus of about 13 tropical American species. It usually grows in cloud forests, wet montane or elfin forests, primarily as an understory species, at elevations from about 1,000 to 2,000 m.

Spores of *Alsophila*, as defined here, are known from the San Sebastian and Paraje Solo formations (as *Cyathea* in both).

Cnemidaria (Figs. 12, 13). Amb oval-triangular, apices rounded; trilete, laesurae straight, narrow, 20–25 μm long, extending ca. $\frac{3}{4}$ to nearly to spore margin, inner margin entire, bordered by occasional faint lip 3–5 μm wide; foveolate, smaller pits (1–6 μm diam.) numerous, irregularly scattered over spore surface, larger pits (12–15 μm)

←

9, ESF S-41.—8–11. *Alsophila*, SL-103, 253', 11, ESF 0-22; SL-103, 253', 4, ESF N-17; SL-103, 253', 2, ESF J-42; SL-103, 253', 16, ESF E-32.—12, 13. *Cnemidaria*, SL-103, 253', 15, ESF Y-24; SL-103, 257', G-12. All photographs taken at 400 \times ; size in microns given in descriptions.

typically 3, symmetrically arranged one each between arms of trilete scar along spore periphery; wall 2–3 μm thick; 40–50 μm .

Cnemidaria is a tropical American tree fern genus of 25 species (Tryon & Tryon, 1982: 209), typically growing in deep-shaded, wet, montane forests, and along stream banks and waterfalls, at elevations up to about 1,500 m.

Spores of *Cnemidaria* have been reported from the San Sebastian (under the name *Hemitelia*), Uscari, and Paraje Solo (as *Hemitelia*) formations.

Cyathea (type 1, Fig. 14). Amb triangular, apices rounded; trilete, laesurae straight, narrow, 30 μm long, extending $\frac{3}{4}$ distance to spore margin, inner margin entire, bordered by faint lip 3–4 μm wide; distal surface micropunctate, proximal surface laevigate; wall 2 μm thick; 58–65 μm .

These fossil spores are similar to spores of *C. petiolaris* (Hook.) Tryon and *C. speciosa* Willd. (Tryon & Tryon, 1982: 207, fig. 20).

Cyathea (type 2, Figs. 15–17). Amb oval-triangular, margin lobate due to projecting sculpture elements, apices rounded; trilete, laesurae straight, narrow, 18–20 μm long, extending $\frac{3}{4}$ to nearly to spore margin, inner margin entire; distal surface with conspicuous, moundlike verrucae, 6–7 μm diam., smooth, proximal surface laevigate; wall 3 μm thick; 45–62 μm .

These spores are similar to those of several species of *Cyathea*, including *C. caracasana* (Kl.) Domin (Tryon & Tryon, 1982: 207, fig. 17).

As defined by Tryon & Tryon (1982: 204) *Cyathea* is a tropical American genus of 40 species, growing primarily in montane and cloud forests, more rarely in lowland rainforests, and typically at elevations between 1,500 and 2,000 m.

Spores of *Cyathea* are known from the Culebra, Cucaracha, La Boca, and Paraje Solo formations.

OPHIOGLOSSACEAE

Ophioglossum (Fig. 18). Amb oval-triangular to nearly circular, apices rounded, margin lobate due to projecting sculpture elements; trilete, laesurae straight, narrow, 32–34 μm long, extending to spore margin, inner margin entire; verrucate,

apices of verrucae rounded to broadly pointed, spore surface between verrucae with irregular to elongated, slitlike punctae; wall 3–4 μm thick; 70–76 μm .

About 10 species of *Ophioglossum* occur in the American tropics. They grow in a wide variety of habitats, often in open woods, savannas, and marshy areas, and usually at elevations between 500 and 3,000 m (Tryon & Tryon, 1982: 36).

Stratigraphic palynologists place *Ophioglossum* spores in the artificial genus *Foveotrilites*, and in the Caribbean region these range from the Upper Cretaceous (Maastrichtian) to Recent. They have not been reported previously from our Gulf/Caribbean Tertiary assemblages.

POLYPODIACEAE

Grammitis (Fig. 19). Amb oval-triangular, apices rounded, margin faintly lobate due to projecting sculpture elements; trilete, laesurae straight, narrow, 17–19 μm long, extending to or nearly to spore margin, inner margin entire; verrucate, verrucae small (ca. 2×1.5 –2 μm), apex often truncate, densely arranged; wall 2 μm thick; 42–46 μm .

There are about 175 American species of *Grammitis*, growing primarily in wet habitats in cloud and elfin forests at elevations typically between 2,000 and 3,000 m. The fossil spores are similar to those of several living species, including *G. kalbreyeri* (Baker) Morton, common in Central America.

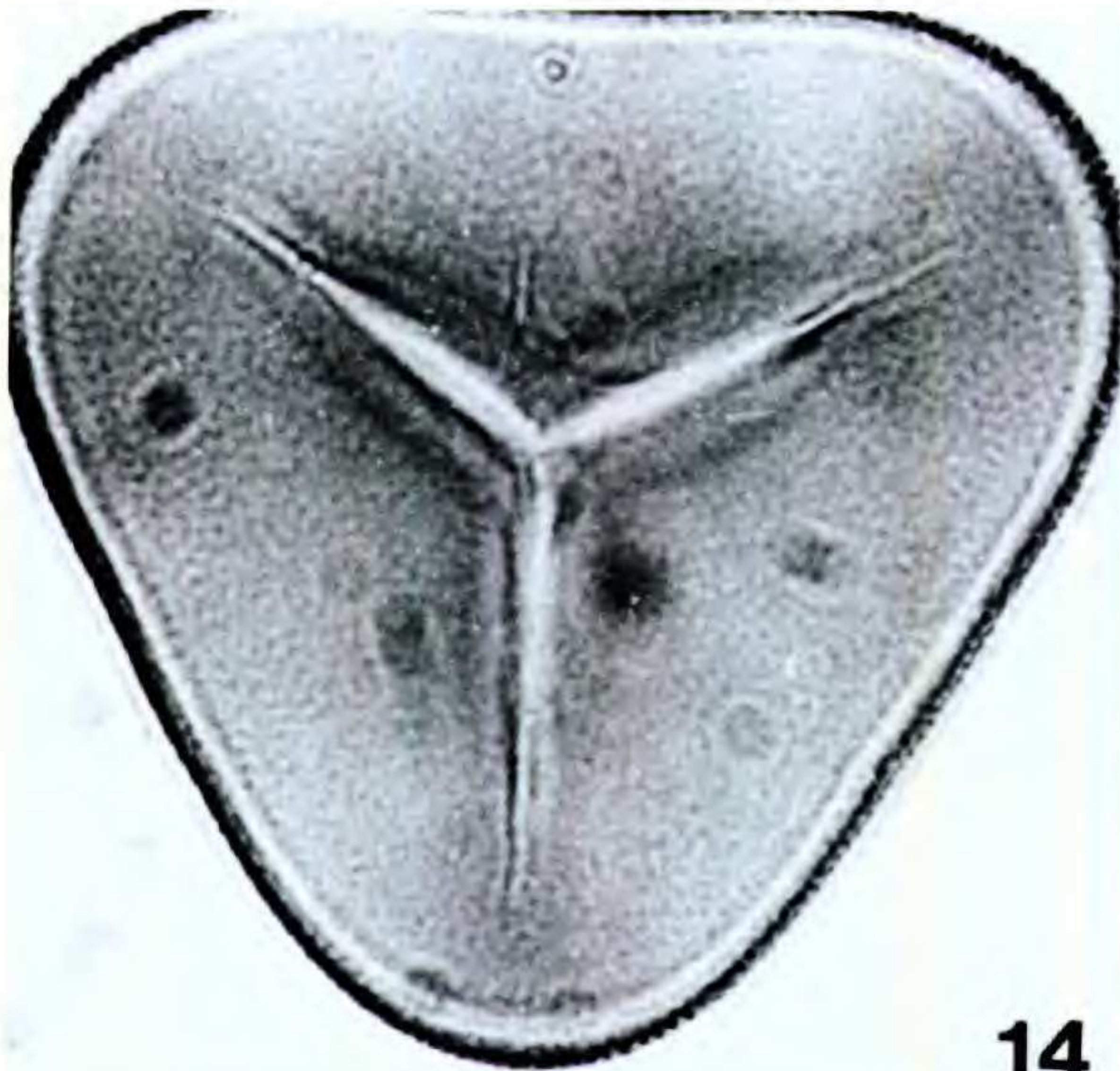
Spores of *Grammitis* have not been reported previously from our Gulf/Caribbean assemblages.

PTERIDACEAE

Ceratopteris (Fig. 20). Amb oval-triangular to circular, apices rounded; trilete, laesurae straight, narrow, 30–32 μm , extending $\frac{1}{2}$ to $\frac{2}{3}$ distance to spore margin; striate, striae in numerous, broad, flat, smooth bands 4–5 μm wide, area between bands 1–2 μm wide; wall 2–3 μm thick; 68–72 μm .

In tropical America *Ceratopteris* consists of two closely related species of floating ferns [*C. pteri-*

FIGURES 14–25. Fossil spores from the Gatun Formation. — 14. *Cyathea* type 1, SL-103, 255.5', 5, ESF V-32. — 15–17. *Cyathea* type 2, SL-103, 253', 9, ESF H-22, D-41; SL-103, 253', 11, ESF N-48. — 18. *Ophioglossum*, SL-103, 253', 6, ESF X-49. — 19. *Grammitis*, SL-103, 253', 6, ESF Q-38. — 20. *Ceratopteris*, SL-48, 162', 1, Q-30. — 21. *Pteris* type 1, SL-103, 253', 1, ESF U-41. — 22. *Pteris* type 2, SL-103, 253', 7, ESF K-24. — 23. *Pteris* type 3, SL-49, 222.5', 1, ESF J-18. — 24. *Pteris* type 4, SL-103, 253', 1, ESF H-47. — 25. *Pteris* type 5, SL-103, 253', 12, ESF M-42.



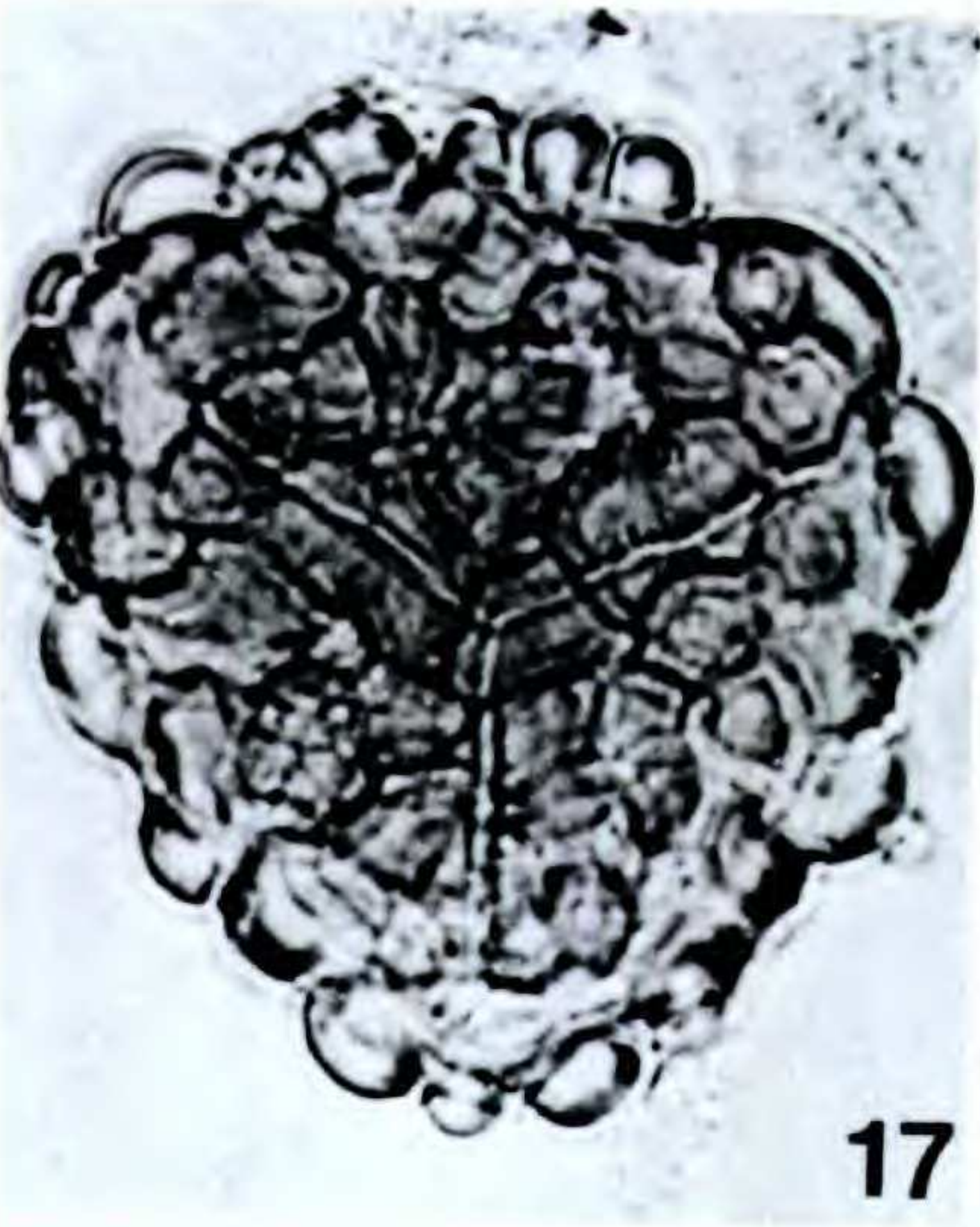
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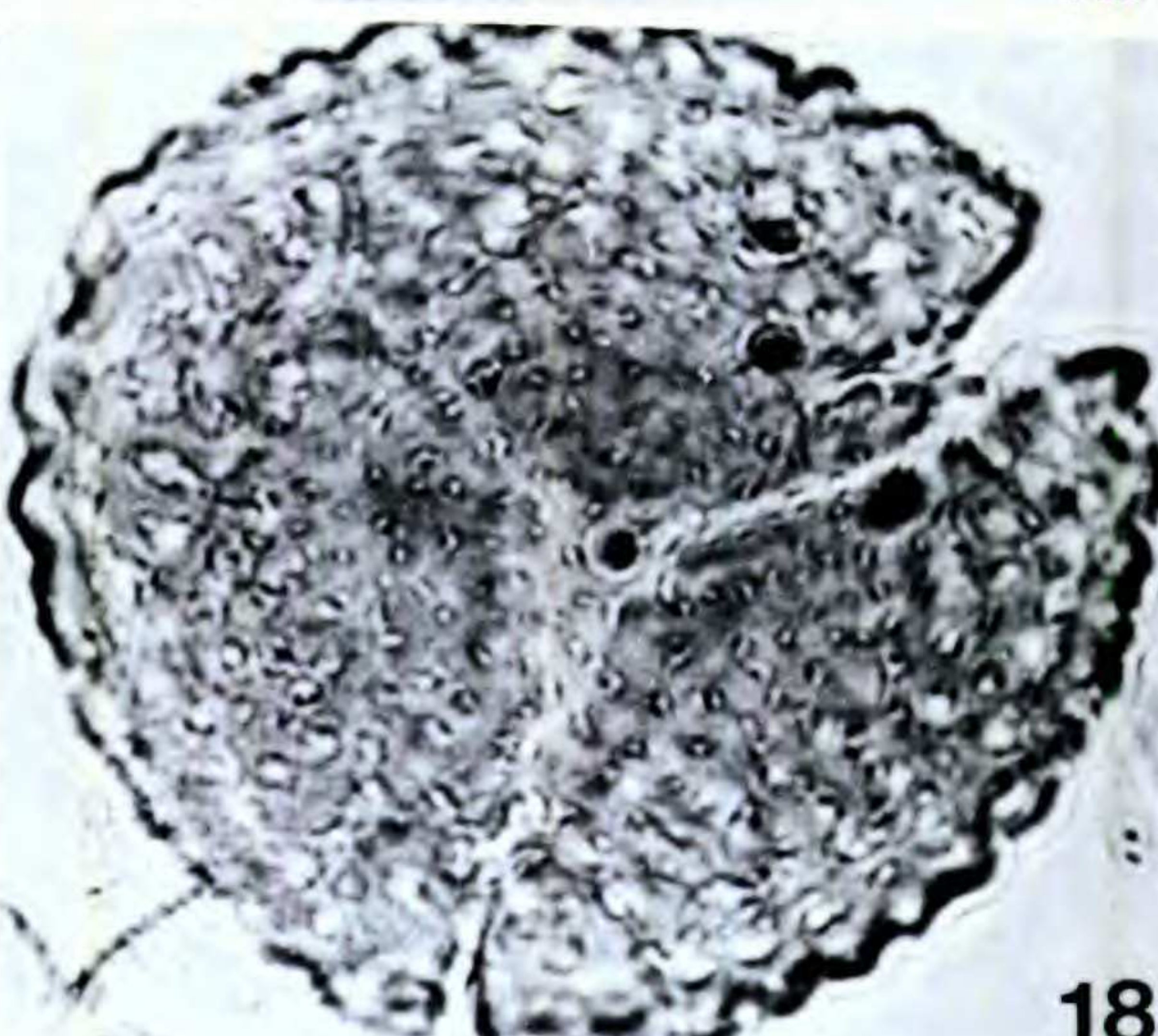
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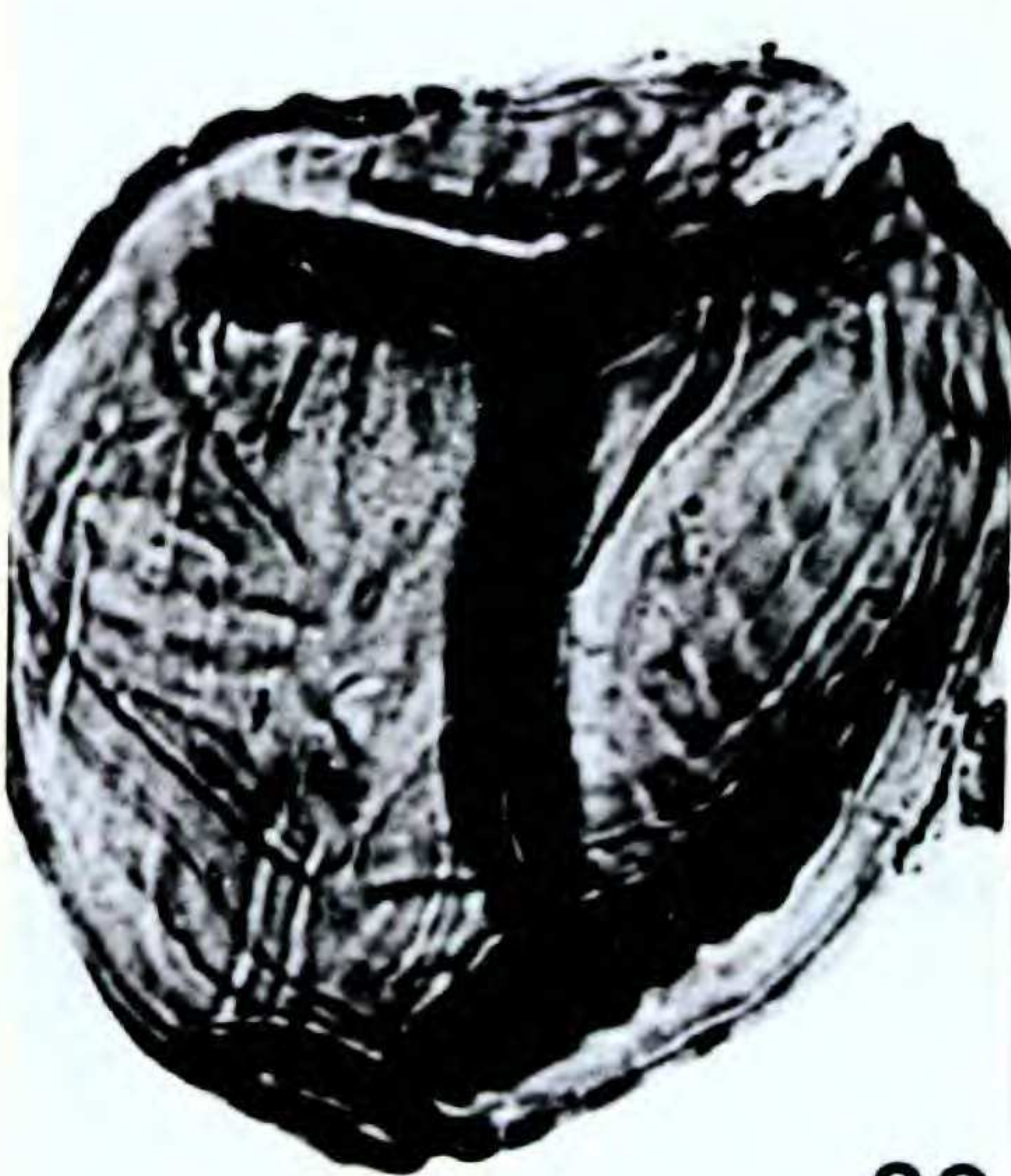
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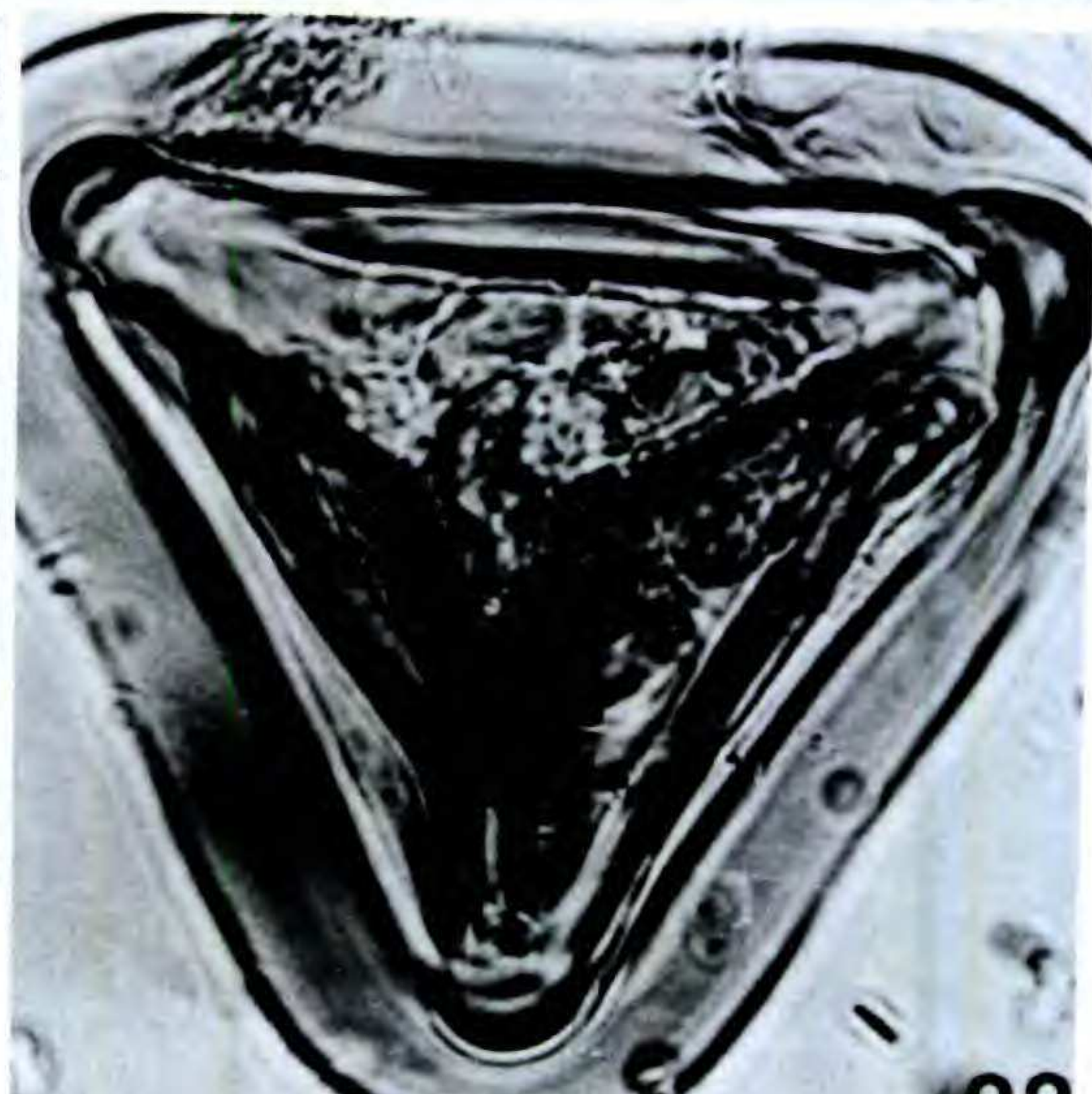
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doides (Hook.) Hieron. and *C. thalictroides* (L.) Brongn.] commonly found in fresh water but occasionally in brackish water habitats. They occur in ditches, lagoons, rivers, lakes, or rooted in wet soil or shallow water, usually between sea level and 300 m (Tryon & Tryon, 1982: 315). No consistent differences could be detected between the spores of the two modern species.

Fossil specimens are known in the stratigraphic literature as *Magnastriatites* and in the Caribbean area were previously listed as ranging from the base of the Oligocene to Recent, but the Gatuncillo report (Graham, 1985) extends the genus back to the middle(?) to upper Eocene. Other records are from the Cucaracha and Paraje Solo formations.

Pteris (type 1, Fig. 21). Amb oval, apices rounded; laesurae straight, narrow, 20–24 μm long, extending to spore margin, inner margin entire; conspicuous flange present, 8–10 μm wide, smooth, outer flange margin entire; distal surface laevigate, proximal surface with few low, flat, shieldlike verrucae; wall 2 μm thick; 52–65 μm .

Pteris type-2 spores (Fig. 22) are larger (80–86 μm), and have a few, large verrucae scattered over the distal surface. Type 3 (59–64 μm , Fig. 23) have numerous, low, flat verrucae with sinuous slitlike spaces between the verrucae. Type 4 (47–66 μm , Fig. 24) have low, smooth, elongated, sinuous verrucae/rugulae. Type 5 (47–51 μm , Fig. 25) have numerous, blocky, angular verrucae. There is a considerable range in variation among modern spores, both within and between species, and these fossil morphotypes cannot be referred consistently to any single species.

About 55 species of *Pteris* occur in the American tropics in a wide variety of habitats. Most are found “in wet forests, at the edge of clearings, in thickets, sometimes in cloud forests or in gallery forests, or occasionally on cliffs,” generally at lower altitudes between sea level and about 2,000 m (Tryon & Tryon, 1982: 338).

The spores are known in the stratigraphic literature as *Polypodiaceoisorites* (Lorente, 1986: 154) and are known from the Gatuncillo, San Sebastian, Uscari, Culebra, Cucaracha, La Boca, and Paraje Solo formations.

OTHER TRILETE FERN SPORES

Several trilete fern spores were recovered that could not be identified. Two of the most common and/or distinctive ones are described below.

Type 1 (Figs. 26, 27). Amb triangular, apices rounded; trilete, laesurae straight, narrow, 20–24

μm , extending to or nearly to spore margin, bordered by faint lip 6–8 μm wide, inner margin entire; spore surface with irregular, slightly raised segments 9–12 μm diam., each with numerous, minute baculae/clavae; wall 3 μm thick; 38–52 μm .

These specimens were originally interpreted as slightly corroded *Cyathea* spores, but ultimately many were recovered with the same characteristic ornamentation. The spore has not been recorded previously in our Gulf/Caribbean Tertiary assemblages.

Type 2 (Fig. 28). Amb circular; trilete, laesurae straight, narrow, 16–18 μm long, extending $\frac{3}{4}$ to nearly to spore margin, inner margin entire; echinate, echinae small (ca. 0.5 μm), numerous and densely distributed; wall 1–2 μm thick; 43–47 μm .

DRYOPTERIDACEAE

Ctenitis (type 1, Fig. 29). Reniform; monolete, laesurae straight, narrow, 19–23 μm long, inner margin entire; echinate, echinae numerous, delicate, narrow, ca. 2 μm long, curved, frequently appearing appressed to spore surface; wall 3 μm thick; 38–40 \times 24–29 μm .

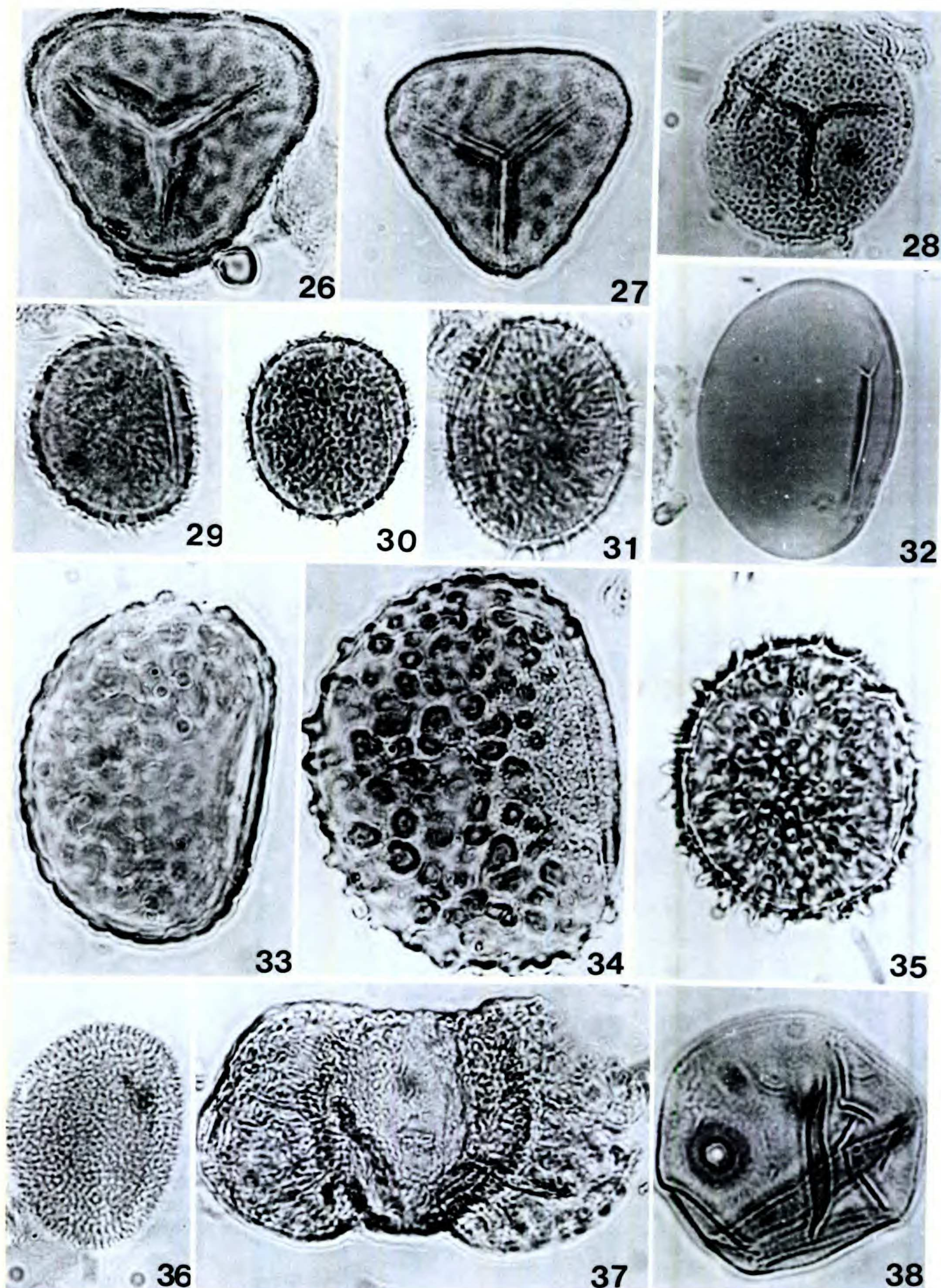
In type 2 (30–38 \times 28–32 μm , Fig. 30) the spines are more straight and do not appear appressed to the spore surface. In type 3 (40–45 \times 34–36 μm , Fig. 31) the spines are longer (ca. 3–4 μm) and somewhat fewer in number. Spores of several modern species also exhibit these variations [*Ctenitis* (= *Megalastrum*) *acrosorum* (Hieron.) Smith & Morgan (1987)], and the fossils cannot be referred to any one species. About 75 species of *Ctenitis* occur in the American tropics, primarily in wet forests, and most frequently at elevations between about 500 and 1,800 m (Tryon & Tryon, 1982: 463). Spores of *Ctenitis* have not been reported previously in our Gulf/Caribbean assemblages.

OTHER MONOLETE FERN SPORES

In addition to *Ctenitis*, several other monolete fern spores were recovered that could not be identified. Several of the most common and/or distinctive ones are described below.

Type 1 (Fig. 32). Reniform; monolete, laesurae straight, narrow, 16–20 μm long, inner margin entire; laevigate; wall 2 μm thick; 55–48 \times 33–39 μm .

Monolete laevigate spores lacking the ornamented perine (*Laevigatisporites*) are common in fossil deposits, ranging from Paleozoic to Recent,



FIGURES 26–38. Fossil spores and pollen from the Gatun Formation.—26, 27. Trilete fern spore type 1, SL-103, 253', 6, ESF 41; SL-103, 253', 2, ESF H-48.—28. Trilete fern spore type 2, SL-103, 253', 9, ESF U-28.—29. *Ctenitis* type 1, SL-103, 253', 10, ESF N-52.—30. *Ctenitis* type 2, SL-103, 257', 1, ESF N-15.—31. *Ctenitis* type 3, SL-103, 253', 12, ESF M-32.—32. Monolete fern spore type 1, SL-103, 253', 1, ESF O-30.—33. Monolete fern spore type 2, SL-103, 253', 1, ESF G-46.—34. Monolete fern spore type 3, SL-103, 253', 9, ESF Q-26.—35. Monolete fern spore type 4, SL-103, 253', 15, ESF T-44.—36. Monolete fern spore type 5, SL-103, 253', 1, ESF T-32.—37. *Podocarpus*, SL-103, 253', 7, ESF J-30.—38. Gramineae, SL-103, 255.5', 5, ESF Q-36.

and are produced by numerous Blechnaceae, Polypodiaceae, and Pteridaceae.

Type 2 ($69\text{--}88 \times 45\text{--}68 \mu\text{m}$, Fig. 33) differs from type 1 in being moderately verrucate, while type 3 ($85\text{--}88 \times 55\text{--}58 \mu\text{m}$, Fig. 34) has more conspicuous verrucae that taper to blunt apices. Both are placed in the artificial genus *Verrucatisporites*, range from Paleozoic to Recent, and are produced by numerous Blechnaceae, Polypodiaceae, and Pteridaceae. Type 4 ($48\text{--}52 \mu\text{m}$ in length, Fig. 35) is similar to some *Ctenitis* spores, but type 4 spores are larger, and the spines ($3 \mu\text{m}$) are more coarse (broader) and the apices are blunt. Type 5 ($42\text{--}48 \times 30\text{--}36 \mu\text{m}$, Fig. 36) has small (ca. $0.5 \mu\text{m}$), fine, clavate to baculate/echinate sculpture elements. None of these can be referred to types presently in our reference collection.

Types 1–3 are common in all our Gulf/Caribbean assemblages, while types 4 and 5 have not been recovered previously.

PODOCARPACEAE

Podocarpus (Fig. 37). Bisaccate; monocolpate, colpus situated between air sacs, margin diffuse, $25\text{--}30 \mu\text{m}$ long, body amb circular, finely verrucate, some sculpture elements elongated forming rugulae, occasionally anastomosing, outer margin lobate, $40\text{--}44 \mu\text{m}$, body wall $1 \mu\text{m}$ thick; air sacs two, hemispheric, $45\text{--}48 \times 36\text{--}39 \mu\text{m}$, large in relation to body size (compared to other vesiculate gymnosperm pollen), reticulate, muri low, narrow (ca. $1 \mu\text{m}$), smooth, lumina irregular in shape and diameter (larger $5\text{--}6 \mu\text{m}$); overall dimensions (including air sacs) $75\text{--}90 \times 40\text{--}50 \mu\text{m}$.

Three species of *Podocarpus* occur in Panama (D'Arcy, 1987): *P. guatemalensis* Standl. (also in Costa Rica and Guatemala), *P. magnifolius* Buch. & N. E. Gray (Guianas, Venezuela), and *P. oleifolius* D. Don. (Costa Rica, Colombia, Ecuador, Peru, Venezuela). The trees grow primarily in mid-to high-altitude cloud forests at elevations between about 1,000 and 2,000 m and are frequently associated with temperate elements such as *Alnus*, *Ilex*, *Myrica*, and *Quercus*. The fossil specimens are similar to *P. oleifolius*, but pollen of the other species are not represented in our reference collection, or by pollinating material at F, MO, and US.

Podocarpus has been reported previously from the San Sebastian, Uscari, and Paraje Solo formations. It is also known from the Oligo–Miocene Simojovel Group of Chiapas, Mexico (Langenheim et al., 1967).

GRAMINEAE (Fig. 38)

Spherical, amb circular; monoporate, pore circular, $3\text{--}4 \mu\text{m}$ diam., inner margin entire, surrounded by annulus $3\text{--}4 \mu\text{m}$ wide; psilate to scabrate; tectate, wall $1\text{--}2 \mu\text{m}$ thick; $36\text{--}44 \mu\text{m}$.

The Gramineae are a stenopalynous family, and the fossil pollen cannot be referred to individual genera. In the stratigraphic literature they are known as *Monoporites*, and in the Caribbean region range from the Paleocene but become abundant beginning only in the lower Eocene. Grass pollen occurs in the Culebra, La Boca, and Paraje Solo formations. It has also been reported (as *Graminidites*) from the Eocene of Cuba (Areces-Mallea, 1988).

PALMAE

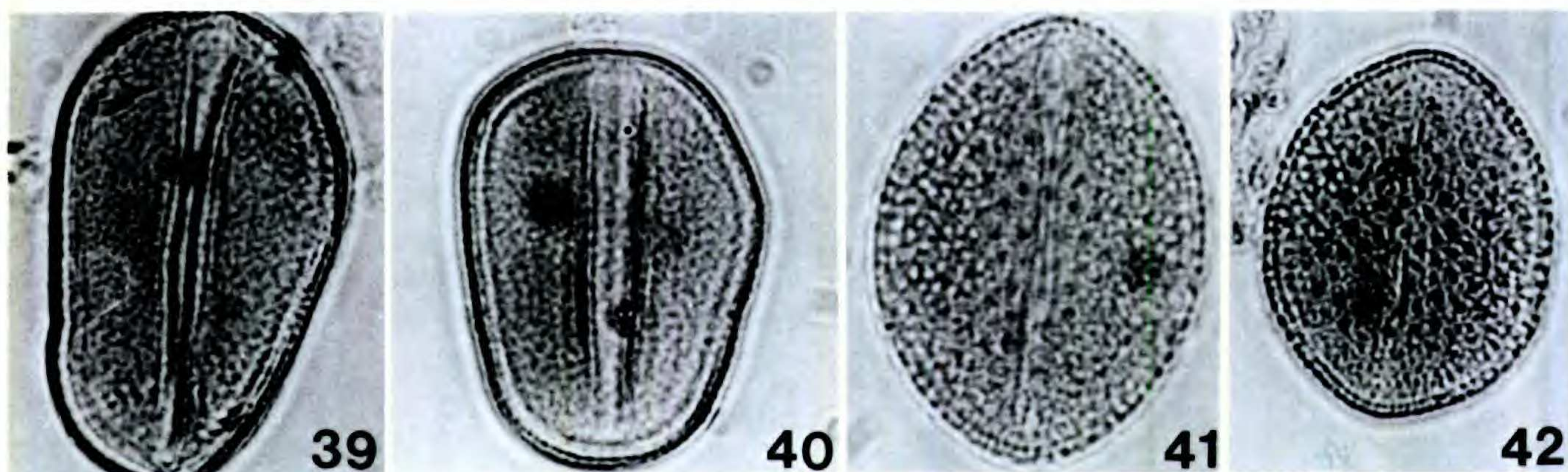
There is considerable diversity in pollen of modern palms (Ferguson, 1986; Thanikaimoni, 1970), but still many types are common to more than one genus and most fossils cannot be identified below the level of family. Two types were recovered from the Gatun sediments.

Type 1 (Figs. 39, 40). Amb cuneiform (wedge-shaped, broadest above equator); monocolpate, colpus straight, $40\text{--}44 \mu\text{m}$ long, extending nearly entire length of grain, sides parallel for most of colpus length, apices blunt to slightly rounded, inner margin minutely dentate; scabrate; tectate, wall $2 \mu\text{m}$ thick; $47\text{--}58 \times 33\text{--}38 \mu\text{m}$.

The pollen is similar to that of *Aiphanes*, *Manicaria*, *Reinhardtia*, and the monocolpate forms of predominately trichotomosulcate genera such as *Acrocomia*. Similar pollen has been reported previously from the Gatuncillo, Culebra, Cucaracha, La Boca, and Paraje Solo formations.

Type 2 (Figs. 41, 42). Amb oval; monocolpate, colpus straight, $33\text{--}35 \mu\text{m}$ long, extending nearly entire length of grains, sides parallel for most of colpus length, apices blunt to slightly rounded, inner margin entire to minutely dentate; reticulate, muri low, smooth, relatively thick ($1.5 \mu\text{m}$) compared to diameter of lumina ($2 \mu\text{m}$), underlying columellae evident giving reticulum faintly beaded appearance, occasional free sexine elements within lumina; tectate-perforate, wall $2 \mu\text{m}$ thick; $43\text{--}45 \times 35\text{--}37 \mu\text{m}$.

This pollen type is similar to that of *Colpothrinax*, *Cryosophila*, and *Neonicholsonia*. Pollen with these characteristics has not been reported previously in our Gulf/Caribbean assemblages.



FIGURES 39–42. Fossil pollen from the Gatun Formation.—39, 40. *Palmae* type 1, SL-103, 253', 7, ESF P-23; SL-103, 253', 6, S-44.—41, 42. *Palmae* type 2, SL-103, 253', 9, ESF Q-23; SL-103, 253', 5, ESF J-48.

In addition to the 31 spore and pollen types described here, 51 kinds of dicotyledonous pollen have been identified from the Gatun Formation, including 13 with no previously known fossil record. There are also 27 unknowns presently under study. This makes the Gatun assemblage, with 110 types, including one unidentified Pyrrophyta (dinoflagellate), the second largest Tertiary fossil flora known from northern Latin America (the largest is the middle Pliocene Paraje Solo flora from Veracruz, Mexico, with approximately 124 types; Graham, 1976). The remaining descriptions, and interpretation of the flora, will be presented in subsequent papers in the series.

LITERATURE CITED

- ARECES-MALLEA, A. 1988. Palinomórfos de la costa del Golfo de Norteamérica en el Eocene medio de Cuba. *Revista Tecnológica* 17: 15–26.
- BARTLETT, A. S. & E. S. BARGHOORN. 1973. Phytogeographic history of the Isthmus of Panama during the past 12,000 years (a history of vegetation, climate, and sea-level change). Pp. 203–299 in A. Graham (editor), *Vegetation and Vegetational History of Northern Latin America*. Elsevier Publ., Amsterdam.
- COOKE, C. W., J. GARDNER & W. P. WOODRING. 1943. Correlation of the Cenozoic formations of the Atlantic and Gulf Coastal Plain and the Caribbean region. *Bull. Geol. Soc. Amer.* 54: 1713–1723.
- CROAT, T. B. 1978. *Flora of Barro Colorado Island*. Stanford Univ. Press, Stanford, California.
- D'ARCY, W. G. 1987. *Flora of Panama Checklist and Index*. Monogr. Syst. Bot. Missouri Bot. Gard., Volumes 17, 18.
- FERGUSON, I. K. 1986. Observations on the variation in pollen morphology of *Palmae* and its significance. *Canad. J. Bot.* 64: 3079–3090.
- GERMERAAD, J. H., C. A. HOPPING & J. MULLER. 1968. Palynology of Tertiary sediments from tropical areas. *Rev. Palaeobot. Palynol.* 6: 189–348.
- GRAHAM, A. 1976. Studies in neotropical paleobotany. II. The Miocene communities of Veracruz, Mexico. *Ann. Missouri Bot. Gard.* 66: 572–576.
- . 1985. Studies in neotropical paleobotany. IV. The Eocene communities of Panama. *Ann. Missouri Bot. Gard.* 72: 504–534.
- . 1987. Miocene communities and paleoenvironments of southern Costa Rica. *Amer. J. Bot.* 74: 1501–1518.
- . 1988a. Studies in neotropical paleobotany. V. The lower Miocene communities of Panama—the Culebra Formation. *Ann. Missouri Bot. Gard.* 75: 1440–1466.
- . 1988b. Studies in neotropical paleobotany. VI. The lower Miocene communities of Panama—the Cucaracha Formation. *Ann. Missouri Bot. Gard.* 75: 1467–1479.
- . 1989. Studies in neotropical paleobotany. VII. The lower Miocene communities of Panama—the La Boca Formation. *Ann. Missouri Bot. Gard.* 76: 50–66.
- , R. H. STEWART & J. L. STEWART. 1985. Studies in neotropical paleobotany. III. The Tertiary communities of Panama—geology of the pollen-bearing deposits. *Ann. Missouri Bot. Gard.* 72: 485–503.
- HOLTUM, R. E. 1964. The tree ferns of the genus *Cyathea* in Australasia and the Pacific. *Blumea* 12: 241–274.
- . 1965. Tree ferns of the genus *Cyathea* Sm. in Asia (excluding Malaysia). *Kew Bull.* 19: 463–487.
- HORN, S. P. 1985. Preliminary pollen analysis of Quaternary sediments from Deep Sea Drilling Project site 565, western Costa Rica. *Initial Reports Deep Sea Drilling Project* 84: 533–547.
- LANGENHEIM, J. H., B. L. HACKNER & A. S. BARTLETT. 1967. Mangrove pollen at the depositional site of Oligo-Miocene amber from Chiapas, Mexico. *Bot. Mus. Leafl.* 21: 289–324.
- LORENTE, M. A. 1986. Palynology and palynofacies of the upper Tertiary in Venezuela. *Dissertationes Botanicae*, Bd. 99, J. Cramer, Berlin.
- OLLGAARD, B. 1987. A revised classification of the Lycopodiaceae s. lat. *Opera Bot.* 92: 153–178.
- SMITH, A. R. & R. C. MORAN. 1987. New combinations in *Megalastrum* (Dryopteridaceae). *Amer. Fern J.* 77: 124–130.
- STEWART, R. H. & J. L. STEWART (with the collaboration of W. P. Woodring). 1980. Geologic Map of the Panama Canal and Vicinity, Republic of Panama. Scale: 1:100,000. U.S. Geol. Surv. Misc. Invest.

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- Map I-1232. [Map also included in Woodring, 1982, Profess. Pap. U.S. Geol. Surv. 306F.]
- THANIKAIMONI, G. 1970. Les palmiers: palynologie et systématique. Inst. Franc. Pondichéry, Trav. Sect. Sci. Tech. XI: 1–286.
- TRYON, R. 1970. The classification of the Cyatheaceae. Contr. Gray Herb. 200: 3–53.
- & A. F. TRYON. 1982. Ferns and Allied Plants, with Special Reference to Tropical America. Springer-Verlag, New York.
- VOKES, E. H. 1983. Additions to the Typhinae (Gastropoda: Muricidae) of the Gatun Formation, Panama. Tulane Studies Geol. Paleontol. 17: 123–130.
- WILCE, J. H. 1972. Lycopod spores, 1. General spore patterns and the generic segregates of *Lycopodium*. Amer. Fern J. 52: 65–79.
- WOODRING, W. P. 1957–1982. Geology and paleontology of Canal Zone and adjoining parts of Panama. Profess. Pap. U.S. Geol. Surv. 306A–F.